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Rice and Sturgeon Lakes Nutrient Budget Study

An Experimental Demonstration of Trophic Interactions Affecting Water Quality of Rice Lake, Ontario

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AN EXPERIMENTAL DEMONSTRATION OF TROPHIC INTERACTIONS AFFECTING WATER QUALITY OF RICE LAKE, ONTARIO

Report prepared by:

K.H. Nicholls
Aquatic Science Section, MOEE
125 Resources Road
Etobicoke, ON

M.F.P. Michalski
Michael Michalski Associates
P.O. Box 367
Bracebridge, ON

and

W. Gibson
Blackburn Hall
Trent University
Peterborough, ON

PREFACE

The Kawartha lakes are a large and economically important system of eight lakes which are located in central Ontario. Sturgeon Lake and Rice Lake are located near the upper and lower ends of the Kawartha Lakes system respectively and both support significant amounts of urban and recreational development. They were chosen for detailed study because of their importance within the system and because both have shown the symptoms associated with excessive nutrient input for several years.

The Rice and Sturgeon Lakes Nutrient Budget Study was initiated to investigate linkages between point and non-point sources of nutrients, water quality, and aquatic life within the lakes and to estimate the impacts of these processes on in-lake and downstream water quality.

The study was supervised by the Rice - Sturgeon Lakes Nutrient Budget Technical Committee which had representatives from the Limnology Section (Water Resources Branch) and Central Region of the Ministry of the Environment, the Trent Severn Waterway (Environment Canada) and the Kawartha Lakes Fisheries Assessment Unit of the Ministry of Natural Resources.

This is one of a series of technical reports. These and the summary report (R/S Tech. Rep. No. 13) will provide a technical basis for the management of the Rice Lake and Sturgeon Lake ecosystems and for the use of land and water resources in the Kawartha Lakes region in general. A list of all reports in the R/S Tech. Rep. series is as follows:

1. Hutchinson N.J., B.J. Clark, J.R. Munro and B.P. Neary 1994. Hydrological data for the watersheds of Rice Lake and Sturgeon Lake.1986 - 1989, 100 pp.

2. Hutchinson N.J., J.R. Munro, B.J. Clark and B.P. Neary. 1994. Water chemistry data for Rice Lake, Sturgeon Lake and their respective catchments 1986-1989, 169 pp.

3. Hutchinson N.J., B.J. Clark J.R. Munro and B.P. Neary, 1994. Nutrient Budget data for the watersheds of Rice Lake and Sturgeon Lake. 120 pp.

4. Ryback, M. and I. Rybak. 1994. Sediment pigment stratigraphy as evidence of long term changes in primary productivity of Sturgeon and Rice Lakes (Kawartha Lakes). 24 pp.

5. Nicholls, K.H., M.F.P. Michalski and W. Gibson. 1994. Trophic interactions in Rice Lake I: An experimental demonstration of effects on water quality.

6. Limnos Ltd. 1994. Partitioning of phosphorus in *Potamogeton crispus*. 22 pp.

7. Limnos Ltd. 1994. Rice Lake Macrophytes: distribution, composition, biomass, tissue nutrient content and ecological significance. 123 pp.

8. Beak Consultants Ltd. 1994. Release of phosphorus from Rice Lake sediments. 31 pp .

9. Limnos Ltd., Michael Michalski Associates and D.J. McQueen. 1994. Trophic interactions in Rice Lake II. Young-of-the-year yellow perch - *Daphnia* interactions, preliminary findings. 101 pp.

10. Badgery, J.E., D.J. McQueen, K.H. Nicholls and P.R.H. Schaap. 1994. Trophic interactions in Rice Lake III: Potential for biomanipulation. 1988 and 1989 .

11. Standke, S. 1994. The zooplankton of Rice Lake and Sturgeon Lakes, 1986-1988, Kawartha Lakes, Ontario .

12. Nicholls, K.H. 1994. The phytoplankton - water quality relationships of the Kawartha Lakes, 1972-1989.

13. Hutchinson, N.J., K.H. Nicholls and S. Maude, 1994. Rice and Sturgeon Lake Nutrient Study: Summary and recommendations.

ABSTRACT

Eight cylindrical enclosures (3m diameter, 2.7m long, V= 20m^3) were installed in eutrophic Rice Lake (Ontario, Canada) in late spring of 1987. Fish (yearling yellow perch (Perca flavescens) and macrophytes (Potamogeton crispus) presence and absence were set at the beginning of the experiment to yield four combinations of duplicate treatments. The main purpose of the experiment was to determine if the phytoplankton, zooplankton, macrophytes and fish species resident in the lake interact to significantly influence water quality.

The presence of fish had the following direct effects: 1) decreased biomass of total zooplankton, 2) decreased number of species in the zooplankton, and 3) decreased average size of several zooplankton taxa, which indirectly contributed to significantly higher phytoplankton biomass. Large Daphnia species were best correlated with this algal response ($r^2 = 0.995$) and were associated with reduced biomass of several algal species including some large forms (Mougeotia, Oedogonium, and several colonial blue-green algae). However, no significant control of late summer growth of the bloom-forming blue-green alga Anabaena planctonica Brun. was achieved by the Daphnia presence-fish absence treatment. The presence or absence of macrophytes had little apparent effect on the trophic interactions among fish, zooplankton and phytoplankton, but influenced greatly the inorganic chemistry (major ions, pH) of the enclosed lakewater through regulation of $CaCO_3$ equilibrium and leaching of cell constituents (especially potassium) during plant senescence. Release of phosphorus to the water column during the die-back of the P. crispus population was not an important phenomenon.

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INTRODUCTION

Rice Lake is a large, shallow lake (101 km^2; mean depth = 2.6 m) in southern Ontario (Fig. 1). It is the lowest lake in the Kawartha-Trent waterway and part of an extensive surface water corridor developed for recreational and navigational use between Lake Simcoe and the Bay of Quinte of Lake Ontario (CORTS 1973). The lake lies in a sedimentary area of till plains and drumlin fields, a consequence of the last glaciation about 11000 years ago. Average annual precipitation (1951-1980) is 85 cm, about 75-80% of which falls as rain. The warmest and coldest months are July and January with average daily temperatures of 19.8°C and -8.9°C, respectively.

Earlier investigations of Rice Lake demonstrated its eutrophic and productive state of the lake (Ontario Ministry of the Environment and Ontario Ministry of Natural Resources 1976). Continued water quality monitoring of the lake during the past decade has suggested that extensive macrophyte growth and excessive blue-green algal densities continue to be the major deterrents to optimal recreational use. However, Rice Lake fish production rates exceeding 25 $kg \bullet ha^{-1} \bullet a^{-1}$ to the recreational fishery are among the highest for natural waters in Ontario (Kawartha Lakes Fisheries Assessment Unit data files) and are due, in part, to the shallow heavily vegetated habitat.

Although perhaps contributing to conflicting uses (navigation vs recreational angling), preservation of a diverse and extensive macrophyte community in Rice Lake is believed to be an important management objective for the lake. Among the factors with high potential to cause a collapse of macrophytes is the excessive growth of epiphytic algae and phytoplankton which could, through shading or other mechanisms, contribute to a collapse of the rooted plant community in the lake (Phillips et al. 1978; Jones et al. 1982; Hough et al. 1989. Excessive accumulation of algae in turn may be enhanced by the loss of grazing organisms such as large Daphnia species, providing other factors such as nutrient supply are optimal for algal growth. The single most important factor affecting large zooplankters is fish predation, and the potential cascading effects on algal-related aspects of water quality through trophic level interactions have been hypothesized and recently demonstrated under experimental and whole-lake conditions [see reviews by McQueen et al. (1989), Northcote (1988) and Lammens et al. (1990)]. The potential complicating effects of macrophytes (mid-summer die-back and nutrient release) on trophic level interactions have not been determined, however.

In Rice Lake, there is some evidence (Ministry of the Environment, unpubl. data) that spring and early summer grazing of phytoplankton by zooplankton (especially Daphnia spp.) may contribute to good water clarity and optimal growth conditions for macrophytes, especially Potamogeton crispus L. (curley leaf pondweed). The early spring growth of P. crispus is believed to enhance larval fish production and survival. The annual die-back of P. crispus in mid-summer is associated with water temperatures >20°C and the resultant development of blue-green algal blooms and associated poor water clarity. The algal blooms may be fuelled by significant inputs of dissolved phosphorus from decaying macrophytes (Smith & Adams 1986).

In order to develop a nutrient management plan for Rice Lake which ensures protection of fish habitat and other human uses, a comprehensive evaluation of the limnology of the lake, including a detailed nutrient mass balance (Hutchinson et al. 1993) was undertaken during 1986-1988. This paper reports on one aspect of this project involving experiments in eight 20 m^3 enclosures used to determine if trophic interactions between indigenous larval fish (yellow perch, Perca flavescens), zooplankton, phytoplankton and macrophytes of Rice Lake are potentially important in controlling phytoplankton density and water clarity. A secondary objective was to determine if zooplankton grazing could significantly influence phytoplankton in the presence of additional nutrients supplied during macrophyte die-back. The experimental design also afforded an opportunity to examine the relative roles of phytoplankton and macrophtes on major ions (potassium, specific conductance). We were fully aware of the problems inherent in our experimental design relating to lakewater enclosure effects and scale distortion (Lundgren 1985; Bloesch et al. 1988) and have deliberately avoided quantifying the trophic interactions and chemical changes as rate processes. We have, however, evaluated the gross differences in several biotic and physical-chemical variables among the enclosures with a view to extrapolating similar cause-effect relationships to the open lake.

MATERIALS AND METHODS

Installation and Maintenance of Enclosures

Early in May, 1987, eight enclosures were installed in the littoral zone of Rice Lake in the lea (east side) of Sheep Island, 0.8 km north of Gores Landing (Fig. 1). Each enclosure consisted of a translucent woven plastic tube, supported at the top by a floatation collar and at the bottom by a sand-filled anchoring tube and skirt. Further stability was achieved by lateral lines fixed to anchors. The floatation collars extended about 0.3 m above the water, to exclude external lakewater. Each enclosure was 3 m in diameter and was installed in approximately 2.7 m of water, giving each a volume of approximately 20 m^3.

Following installation, the enclosures were randomly numbered and the above-ground portions of all macrophytes were removed from four of the eight enclosures (numbers 3 to 6). Fish were removed from all enclosures by electroshocking, and approximately 100 yearling yellow perch (4 cm to 6 cm in length) were placed in each of enclosures 1 to 4. This established the four different macrophyte/fish treatments (Table 1). Macrophyte regrowth in enclosures without macrophytes (3, 4, 5 and 6) was not significant, but was removed when observed. P. crispus plants began die-back about mid-June when the first floating stems were observed. Plants deteriorated first near their bases, so the status and progression of senescence was difficult to assess. Die-back was completed about mid-July. Some growth of macrophytes (mainly Myriophyllum spp.) occurred after P. crispus die-back in all four enclosures (1,2,7 and 8). These plants were not removed and maximum biomasses achieved were estimated to be <10% of P. crispus biomass.

From May 13 through September 14, the enclosures were serviced daily. Repairs were made whenever any damage was seen. More thorough inspections by divers were made on July 22. Regrowth of P. crispus in enclosures 3 to 6 was minimized by removing all new visible stems. Approximate counts of enclosed perch were made daily, and young-of-the-year perch apparently lost through small tears in the fabric were regularly replaced. Some young bass (probably smallmouth bass, Micropterus dolomieu) were found over a two-week period in June. On July 16, a number of these fish were seen in enclosure 7 and a corresponding deterioration in water quality was noted; on July 22 divers found an opening at the bottom of the enclosure. This was repaired, and the fish which had earlier gained entry to the enclosure (i.e., either hatched in situ or gained access through the gap) were removed. Most of these problems with the enclosures were minor and effects on water quality were believed to be minimal with the exception of the late July results from enclosure No 7. Emphasis here is on presentation of May-June data, when problems with enclosure integrity were minimal.

Water Sampling and Analytical Methods

From May 13 through September 14, the following parameters were measured weekly at each of the eight enclosures and at a nearby open water reference site: dissolved oxygen with depth (Winkler calibrated probe), temperature with depth, light attenuation (submarine photometer) and Secchi disc visibility. At the same times and locations, water samples were collected for: total and soluble reactive phosphorus, pH, conductivity, potassium, and chlorophyll a. All parameters were measured every one to two days during the major period of P. crispus die-back (June 9 to June 23); in this regard, a total of seven to eight measurements were made for each of these parameters, at each site, during this period. Additionally, water samples were collected once every two weeks for the following parameters: ammonium, total Kjeldahl and nitrate nitrogen, and phytoplankton and zooplankton species and abundance.

Before water samples were taken from the enclosures, the contents of each enclosure were gently mixed with a paddle. Water samples were then collected from both the upper and lower portions of the water column at four locations within the enclosure, approximately equally spaced from each other and from the side walls. Hence, a total of eight Van Dorn bottles was collected from each enclosure. The eight samples were mixed in a large plastic pail from which single subsamples were taken for the various analyses. Phosphorus samples were collected in 50 mL glass screw cap test tubes; the remaining chemical samples were collected in 300 mL polycarbonate containers. Phytoplankton samples were also collected in 300 mL polycarbonate bottles and preserved with Lugol's iodine solution. Samples for chlorophyll *a* were collected in 500 mL glass bottles and immediately stabilized with about 0.5 cc magnesium carbonate suspension and wrapped in tin foil to minimize light effects. From the remaining water, 20 L were passed through a zooplankton net bucket constructed from a wide-mouth plastic bottle having 80 μm mesh windows; the resulting concentrated zooplankton sample was washed with a sugar-formalin preservative into a 300 mL polycarbonate bottle.

In situ dissolved oxygen and temperature readings were taken using a YSI meter (Model 54ARC), calibrated against a standard Winkler titration prior to each sampling run. Water clarity was determined with a Secchi disc, and light transmission was measured with a LI-COR LI-1000 Datalogger. A YSI conductance meter (Model 32) was used to measure conductivity, with all readings temperature adjusted to 25°C. The pH of air equilibrated samples was determined using a Radiometer pH meter (Model 29). Ammonia nitrogen and total Kjeldahl nitrogen were determined by the method of Golterman *et al.* (1978). Nitrate nitrogen concentrations were determined using the modified sodium salicylate method outlined by Kalff & Bentzen (1984).

Soluble reactive phosphorus was determined on 0.45 μm membrane filtrate using Langer & Hendrix (1982). Total phosphorus was measured after an autoclave digestion with persulphate.

Samples taken for chlorophyll *a* were filtered onto glass fiber filters within a few hours of being collected and stored frozen pending analysis. Chlorophyll was extracted with ethanol and analyzed colourimetrically, with absorbency measurements at 750 nm (turbidity correction), 665 nm and 649 nm. Chlorophyll *a* concentrations were then calculated from:

$$\text{Chl } \underline{a}\ (\mu\text{g/L}) = \frac{(13.7\ \text{A665} - 5.76\ \text{A649})\text{v}}{\text{V1}}$$

where v = volume of extractant (mL), V = volume of lake water filtered (L), and l = length of light path (cm).

Phytoplankton samples were pooled prior to analysis; the samples collected during May and June from enclosure treatment pairs were composited and analyzed, as for a single phytoplankton determination. Similarly, all samples collected from like enclosure pairs during August and September were composited and analyzed. Inverted microscopy (Nicholls & Carney 1979) with Utermöhl - type counting chambers was used, and all results were expressed as cell volumes.

Zooplankton determinations (i.e., density, mean length and weight, and biomass) were as described by Yan & Mackie (1987) using a computerized routine for biomass calculations (ZEBRA programme). A minimum of 250 animals were identified and enumerated in each sample. Copepodids and nauplii were included in the enumeration, but were not identified.

RESULTS

The effect of zooplankton control by fish was dramatic. By early June there were obvious differences in phytoplankton density and water clarity. By mid June, enclosure No.7 had developed an anomalous turbid, green colour apparently owing to the accidental introduction of larval fish (see Methods section). In general, enclosures without fish were noticeably clearer than those with fish and the presence or absence of macrophytes had no major influence on this effect (Figs. 2, 3).

The initial water chemistry of each enclosure measured in mid May was not identical. For example, the differences in initial specific conductance between enclosures were as high as 20% and were possibly related to the patchiness of macrophyte distribution and associated localized calcite precipitation in the study area. In order to compare the results from the different enclosure treatments, each set of data from the paired treatments was referred to a common baseline calculated as the average of concentrations measured on May 13 and May 17 (initial concentrations) of all enclosures being compared. Because there was excellent agreement between the duplicate enclosures of each treatment (e.g., Fig. 4), the data from pairs of like treatments were averaged for comparison to other treatments.

Potassium concentrations in all treatments and the open lake showed the same trend with generally constant levels at about 0.3-0.5 $mg \cdot L^{-1}$ during May and early June followed by a rapid rise to a peak of about 1.1-1.4 $mg \cdot L^{-1}$ by late June or July. The late summer period was characterized by a slow decline to about 1 $mg \cdot L^{-1}$ by mid-September (Fig. 4).

There were significant differences (analysis of variance, $\alpha = 0.05$) between treatments. Throughout most of June and July, potassium levels in enclosures with macrophytes averaged about 0.2 $mg \bullet L^{-1}$ higher in enclosures without fish than in enclosures with fish (Fig. 5), but the rate of increase of potassium in both treatments was about the same (25-30 $mg \cdot m^{-3} \cdot day^{-1}$). Maximum concentrations of 1.4 $mg \cdot K \cdot L^{-1}$ (or 1.1 $mg \cdot L^{-1}$ above initial baseline) were achieved by early July in enclosures lacking fish (Fig. 5).

The potassium rise at the adjacent reference (non-enclosed) site in the lake (Fig. 6) followed the same trend, but the maximum concentrations in July were 10-30% lower than those observed in the enclosures with macrophytes. In enclosures without macrophytes, the difference in average potassium levels (fish vs no fish) was not statistically significant ($\alpha = 0.05$). The maximum concentrations were achieved in early August and the rate of increase (11 $mg \cdot m^{-3} \bullet day^{-1}$) was less than half of that measured in the enclosures with macrophytes. Similar differences among treatments were found in the specific conductance data. Again the effect of fish presence/absence was dramatic in the presence of macrophytes but was not detectable in enclosures lacking macrophytes (Fig. 7). Coincident with the June rise in conductivity in enclosures 7 and 8 (macrophytes present, fish absent), pH declined from 8.2 to 7.2. Enclosures lacking macrophytes did not show this decline (Fig. 8).

In contrast to the dramatic increase in potassium concentrations associated with the P. crispus die-back in enclosures, only minor increases were observed in total phosphorus concentrations. These increases extended well past the June-July P. crispus die-back period into August and September (Fig. 9) and the rates of increase were not significantly different among treatments with the exception of enclosures lacking macrophytes where the absence of fish was associated with an increase in total P exceeding that in enclosures with fish by about 40% (Table 2).

Based on calculations of tissue-bound potassium in P. crispus, the 400 $\mu g\ K \cdot L^{-1}$ increase attributable to P. crispus decomposition (i.e., the difference between yields of dissolved K in enclosures with and without macrophytes) represented 67% of the potential 600 $\mu g\ K \cdot L^{-1}$ (Table 2). In contrast, the phosphorus increase attributable to P. crispus decomposition represented only between zero (fish absent) and 2.7% (fish present) of the phosphorus initially available in P. crispus tissue (Table 2).

Zooplankton and Phytoplankton

The presence or absence of zooplanktivorous yellow perch had a dramatic effect on the number of taxa, individual sizes and total biomass of zooplankton in the enclosures. Generally, between 5 and 15 taxa were found in each sample. However, those enclosures lacking fish contained significantly greater numbers of taxa ($\alpha = 0.05$) than those to which zooplanktivores had been introduced (Table 3). This was the case for both the early summer and the late summer periods.

Small cladocerans (Bosmina longirostris, Chydorus sphaericus, Ceriodaphnia sp.) were abundant and occasionally comprised more than 80% of the total zooplankton biomass. Although represented in smaller numbers, Daphnia pulex, Daphnia galeata mendotae and Daphnia retrocurva also contributed significantly to total biomass in the fishless enclosures, owing to their large body sizes. Several cyclopoids (species of Cyclops, Eucyclops, Mesocyclops and Tropocyclops) were also important, but the bulk of the cyclopoid biomass was often contributed by immature (unidentified) copepodid stages. The maximum densities of 20 of the 35 identified taxa occurred in the enclosures from which zooplanktivorous fish had been excluded (Table 4). Not only were the maximum recorded densities for most species higher in enclosures excluding zooplanktivores, but their average individual sizes were larger (Table 5).

Zooplankton effects on phytoplankton biomass and chlorophyll a concentrations were directly related only to Daphnia biomass and no other taxonomic or functional zooplankton group. During the May-June period, maximum phytoplankton and chlorophyll a levels were found in enclosures 1,2,3 and 4 (zooplanktivores present), but these enclosures had intermediate biomasses of both total Cladocera and total zooplankton (Fig. 10a, 10b). In contrast, the relationships between total Daphnia biomass and phytoplankton and chlorophyll were well defined (Fig. 10c) with Daphnia biomasses in the range 0-160 mg•m^{-3} influencing phytoplankton over a 4-5 fold range. These relationships are clearly defined by least squares fits to power curves:

$Y_1 = 17.5\ (X^{-0.78})\quad (r^2 = 0.995)$
and $Y_2 = 5.6\ (X^{-0.31})\quad (r^2 = 0.963)$
where Y_1 is phytoplankton biovolume (mm^3•L^{-1}),
Y_2 is chlorophyll a concentration (μg•L^{-1}), and
X is Daphnia biomass (mg•m^{-3}, dry mass).

Although the highest Daphnia biomasses during August-September were still associated with the lowest phytoplankton densities, the overall relationships were not as well defined for the late summer period as for the May-June period.

Several phytoplankton taxa appear to have been grazed significantly by Daphnia. During May-June, all major groups of algae except cryptophytes showed much lower average biomasses in enclosures 5, 6, 7 and 8 than in the enclosures to which zooplanktivores had been added (Table 6). Even colonial (filamentous) forms (Melosira, Mougeotia, Oedogonium and Oscillatoria species) appear to have been utilized to a high degree during both early summer and late summer periods.

A major shift to blue-green algae occurred during the mid to late summer (as is typical of Rice Lake). At this time, the bulk of the total biomass in all enclosures and the lake was contributed by Anabaena (mainly Anabaena planctonica Br.). The ill-defined relationship between phytoplankton and Daphnia for the August-September period appears to have been a direct result of the dominance of the algal community by Anabaena, densities of which actually increased nearly two-fold in the absence of zooplanktivores in enclosures 5, 6, 7 and 8 (Table 6). Much lower Anabaena biomasses were present during May-June, but a similar Anabaena increase was found in enclosures lacking zooplanktivores (Table 6).

DISCUSSION

Major Ions

The differences in conductivity observed among treatments is a classic demonstration of the dominant role of macrophytes in the regulation of $CaCO_3$ equilibrium. The assimilation of equilibrium CO_2 and the precipitation of calcite by macrophytes during May and early June resulted in the initial declines in conductivity. With the senescence of the macrophytes and the associated generation of free carbon dioxide, dissolution of $CaCO_3$ led to increases of $Ca(HCO_3)_2$ in solution and corresponding increases in conductivity.

The influence of Daphnia (via fish predation) on this sequence was dramatic. Fish control of Daphnia probably contributed to a lower rate of calcite precipitation under the more turbid conditions associated with higher algal densities in enclosures 5 and 6. Additionally, during plant decomposition, lower concentrations of aggressive free CO_2 accumulated owing to assimilation by algae. In the fish-free enclosures, where algae control by Daphnia resulted in lower rates of CO_2 assimilation by algae, more dissolution of $CaCO_3$ was achieved and hence, higher specific conductance was measured. Although direct evidence for the algae - CO_2 effect is not available (free CO_2 was not measured), the pH data offer strong support for these conclusions. During June, coincident with the rise in conductivity, enclosures 7 and 8 (macrophytes present, fish absent) showed a decline of one full pH unit, which was in contrast to the uniformly constant pH levels in enclosures lacking macrophytes.

The loss of potassium from senescing P. crispus occurred early in the period of plant decline coinciding with an increase in the rate of respiration relative to photosynthesis (with associated net accumulation of free CO_2 and a decline in pH). The increase in specific conductance (HCO_3 production from marl dissolution) lagged behind the initial potassium increases and pH declines by 1-2 weeks in the enclosures and in the adjacent lake water. The generally higher potassium levels observed in enclosures 7 and 8 in the absence of fish may indicate a larger initial potassium reserve in macrophyte tissue in the high Daphnia/low algae enclosures resulting from lower potassium uptake by algae. Then, under these conditions of low algal uptake controlled by Daphnia (per enclosures 7 and 8) and macrophyte decomposition and associated potassium release, higher accumulations of potassium in solution would be expected.

In the enclosures without macrophytes, no significant difference in potassium levels with and without Daphnia were observed, thus confirming the dominant role of macrophytes (as opposed to algae) in potassium uptake and release. The slow and much less dramatic increase in K levels in the enclosures without macrophytes during the June-July period, may reflect, 1) some low level response of limited plant regrowth in enclosures from which plants had been initially removed, and 2) a chronic low level diffusion of potassium from the ambient lake water through the enclosure walls. However, these "dilution" influences were relatively minor and did not detract from the overall dramatic bio-chemical responses attributable to the major treatments (with/without macrophytes and with/without fish).

Phosphorus

While there may still be conflicting views on the impact of aquatic macrophytes on phosphorus cycling in lakes (see reviews by Webster & Benfield 1986; Carpenter & Lodge 1986; Granéli & Solander 1988), considerable recent evidence confirms that macrophytes may not directly cause a pulse loading of phosphorus to lakewater during die-back. Welch et al. (1988) showed that the decomposition of a dense population of Elodea did not contribute significantly to the total supply of phosphorus to Long Lake (Washington). Several laboratory and lake enclosure studies of nutrient dynamics associated with macrophyte senescence have shown that phosphorus released during die-back was quickly incorporated into bottom sediments (Nichols & Keeney 1973; Howard-Williams & Allanson 1981; Boston & Perkins 1982; Best et al. 1990).

In contrast, Landers (1982) showed a significant increase in phosphorus concentrations associated with late summer decay of Myriophyllum in enclosures in an Indiana lake. This supply of phosphorus apparently caused a large increase in phytoplankton growth (about 6x higher than in control enclosures without Myriophyllum). Factors such as season, plant species, availability of complexing materials and other organisms and physical-chemical conditions all must have a bearing on the fate of phosphorus released from senescing macrophytes.

Few studies have examined nutrient loss during decay of P. crispus specifically. Rogers & Breen (1982) determined the effects of drying on mass and nutrient loss of P. crispus in South Africa, and Michaud et al. (1979) found only a small increase in lakewater concentrations of phosphorus following a heRbicide treatment of P. crispus.

In 1987, a detailed intensive sampling of 43 sites in Rice Lake (daily from June 8 to June 18) failed to detect an increase in total phosphorus associated with the P. crispus die-back. A follow-up study in 1988 on Rice Lake P. crispus throughout the growing season, and the senescence and die-back periods showed that only small losses (about 25%) of phosphorus from stem and leaf tissue occurred. There was no evidence of transfer of phosphorus to roots or reproductive structures. Turions contained a similar concentration of phosphorus as found in vegetative tissues, at 0.13 - 0.26% of dry mass (Limnos Ltd. 1993). Because P. crispus in Rice Lake appears to die back first in the lower parts of the plant (lower stems weaken, the plant collapses and falls to the sediment), the final stages of decay must result in release of phosphorus which is quickly adsorbed by surface sediment complexes. However, this decomposition process is apparently slow. On July 25, 1988, approximately one month after die-back, a sample of decomposing P. crispus from the bottom of Rice Lake still contained 0.11% phosphorus (of dry mass).

In the Rice Lake enclosures, the increase in total P was significant, but maximum concentrations occurred in late August and early September, several weeks after the P. crispus decline. Although late summer maxima were typically 2 to 5 times higher than the spring concentrations, the highest concentrations represented only a minor fraction of the total P potentially available in healthy plant tissue early in the season. More importantly, the phosphorus increases were just as significant in enclosures lacking macrophytes; therefore a different source was implicated. Since all treatments had either zooplanktivores or zooplankton, and because both groups are well known phosphorus processors (consumption of particulate P and excretion of dissolved, algal-available P; Andersson et al. 1988; Brabrand et al. 1990) it has not been possible to separate these potential sources from a potential sediment source mediated by microorganismic decomposition of sediment organic matter. Release of phosphorus from iron hydroxide complexes is not a likely source since the water column of all enclosures was well oxygenated immediately above the sediments. It is apparent then, that mid-to-late summer blooms of algae in Rice Lake are not triggered directly by phosphorus released during the Potamogeton crispus decline. It is likely that some phosphorus of macrophyte origin is released through microbial processing of the macrophyte litter later in the summer and made available either directly to the developing phytoplankton blooms, or indirectly through trophic interactions. The latter mechanism could involve consumption of progressively larger particles by components of the Rice Lake food chain and ultimate excretion of dissolved phosphorus by macrozooplankton and small fish. This might explain the significantly higher Anabaena densities found in Rice Lake enclosures with fish.

Biotic Interactions

One main purpose of the enclosure experiment in Rice Lake was to determine if the natural assemblage of planktonic species could be altered by a dominant indigenous fish species (young yellow perch). It was not known if significant trophic interactions existed between the species of algae, zooplankton and fish present in Rice Lake or if these relationships could be manipulated to achieve a significant alteration of the phytoplankton of the lake. It was anticipated that a comprehensive water quality management plan for Rice Lake might include the management of fish community structure through management of harvest, plantings and the habitats of selected species (Hosper & Jagtman 1990; Langeland 1990; Duncan 1990). Such an approach could complement other parts of the perceived plan relating to nutrient control from sources within the drainage basin.

Recent indications are that this "ecosystem approach" to the management of lakes, first advocated by Shapiro et al. (1975), is now getting serious attention (Benndorf 1987, 1990; Benndorf et al. 1988; Van Donk et al. 1990; Moss et al. 1988). McQueen (1990) and Lammens et al. (1990) have concluded that the potential for algae control via fish community manipulation is greater in shallow lakes (such as Rice Lake) than in deep lakes. The findings of the Rice Lake work have clearly indicated the potential for strong food web interactions (i.e., the "right" species are present, especially during early summer). Downstream from Rice Lake in the upper Bay of Quinte, where many of the same planktonic species are found, highly significant relationships exist between the abundance of alewife and white perch and phytoplankton density (Nicholls & Hurley 1989).

One surprising finding from the Rice Lake work was the measure of control of large colonial and filamentous algae achieved in the absence of fish. In particular, the observed reduction of Aphanizomenon, Lyngbya, Microcystis and Oscillatoria by zooplankton is an apparent contradiction of the widely held belief that blue-green algae in general are not suitable food items (Porter 1977; Briand & McCauley 1978; Lampert 1981). More recently however, Nicholls and Hurley (1989) hypothesized that control of large colonial and filamentous phytoplankton species may result from consumption of early life stages (small colonies and short trichome lengths) of these algae. In support of this, Dawidowicz (1990) has shown that Daphnia will consume some species of filamentous blue-green algae if filaments are short($<30\mu$m).

Since the major water quality problems in Rice Lake are related mainly to the late summer blue-green algae blooms, any attempts to "biomanipulate" water quality should probably be preceded by more detailed experiments on the bioenergetics of the major components (Anabaena, Daphnia and yellow perch). It is possible that factors conducive to high Anabaena production (e.g., nutrient supply, shallow, warm water, preferential grazing of other more desirable algae by Daphnia) may result in such a high production rate of Anabaena that it is bioenergetically impossible for the major zooplankton grazing elements to achieve equilibrium at a level which results in measurable lake-wide Anabaena control. It is also possible that lack of Anabaena control through zooplankton grazing may result from direct toxicity effects of this organism on potential crustacean consumers (de Bernardi & Guissani 1990). In addition, trophic interactions on a lake-wide scale may be complicated in Rice Lake by the extensive macrophyte beds which introduce indirect and variable effects relating to shading, resuspension of nutrients, complexities of fish habitat and survival, zooplankton refuge availability and competition for nutrients (McQueen 1990; Ozimek *et al*. 1990; Irvine *et al*. 1990; Moss 1990; Shapiro 1990).

A further complicating factor in predicting possible water quality benefits to be derived from fish community alterations relates to the inevitable invasion of the zebra mussel (*Dreissena polymorpha*. This bivalve has become well established only recently in the Laurentian Great Lakes (Hebert *et al*. 1989) and now threatens much of Ontario's inland waterways, including the Kawartha Lakes - Trent River system, of which Rice Lake is a part. *D. polymorpha* has recently caused major reductions in phytoplankton and chlorophyll *a* concentrations and marked increases in water clarity in Lake Erie (Leach 1993; Nicholls and Hopkins 1993). Major whole-lake fisheries manipulations at this time in Rice Lake to achieve water quality benefits would therefore be premature in the face of the pending zebra mussel invasion since the effects of the mussels on other aquatic components of the Rice Lake ecosystem are largely unpredictable at this time. It is therefore recommended that available scientific and technical resources be directed towards an adequate inventory and monitoring of limnological and fisheries information for Rice Lake, realizing that manipulations of certain biotic components (macrophytes, fish, zebra mussels) are options for future water quality management strategies.

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Table 1 Treatment regimes in experimental enclosures (3 m diameter, 20 m^3 volume) installed along the S.E. shore of Sheep Island in Rice Lake.

Enclosure No. (and Key)		Treatment
1, 2	(+M, +F)	macrophytes present, zooplanktivores present
3, 4	(-M, +F)	macrophytes removed, zooplanktivores present
5, 6	(-M, +F)	macrophytes removed, zooplanktivores removed
7, 8	(+M, -F)	macrophytes present, zooplanktivores removed

Table 2 Spring-summer increases in potassium and phosphorus measured in enclosures with and without macrophytes and with and without zooplanktivorous fish. Predicted increases based on plant density and elemental composition of Potamogeton crispus in Rice Lake are also given.

	Measured increase (mg/L)		***Predicted increase (mg/L)**	
Macrophytes Present	**K**	**P**	**K**	**P**
+fish (enclosures 1&2)	1.0	0.050	0.60	0.543
-fish (enclosures 7&8)	1.2	0.060	0.60	0.543
mean =	**1.1**	**0.055**	**0.60**	**0.543**
Macrophytes Absent				
+fish (enclosures 3&4)	0.7	0.035	0	0
-fish (enclosures 5&6)	0.7	0.060	0	0
mean =	**0.7**	**0.047**		

* Predicted values assume 1) total release of elements to the water column from plant tissue during die-back and no loss to sediments or to enclosure walls, 2) no influence of fish (through food chain or direct effects), 3) a wet mass of 2 $kg \cdot m^{-2}$, a dry mass of 0.16 $kg \cdot m^{-2}$, an ash-free dry mass of 0.13 $kg \cdot m^{-2}$, and a total above ground tissue-bound P mass of 1.47 $g \cdot m^{-2}$, and K mass of 1.625 $g \cdot m^{-2}$ (all values based on several replicates from adjacent areas of Rice Lake with comparable growth of P. crispus).

Table 3 Average numbers (± 1 St. Dev.) of zooplankton taxa in enclosures with (+F) and without (-F) zooplanktivores and with (+M) and without (-M) macrophytes. Also included are data from the reference (non-enclosed) lake station. Data underscored by the same line are not significantly different ($\alpha = 0.05$) according to analysis of variance and least significant difference tests.

Number of Taxa (May - June)

Enclosure	VII	VIII	VI	LAKE	V	I	III	II	IV
	+M-F	+M-F	-M-F		-M-F	+M+F	-M+F	+M+F	-M+F
	15.2 ±2.8	14.2 ±3.4	12.6 ±3.3	11.6 ±3.6	11.2 ±0.8	10.5 ±1.9	7.8 ±2.8	7.6 ±2.3	5.8 ±1.2

Number of Taxa (May-Sept.)

Enclosure	VII	VI	V	VIII	LAKE	II	I	III	IV
	+M-F	-M-F	-M-F	+M-F		+M+F	+M+F	-M+F	-M-F
	14.2±2.0	13.2±2.7	13.2±2.0	13.0±2.4	11.3 ±4.0	10.5 ±3.7	10.3 ±2.3	10.3 ±3.0	7.2 ±1.7

Table 4 Maximum recorded densities (number per m^3) of zooplankton species in the Rice Lake enclosures. (Enclosures keyed as in Table 1.)

Taxon	#/m^3	Enclosure No. (and key)	Date
Acroperus *harpae*	8,000	1(+M+F)	Sept. 7
Alona affinis	500	3(-M+F)	Aug. 26
Alona guttata	3,000	4(-M+F)	Sept. 7
Alona sp.	4,000	2(+M+F)	Aug. 26
Bosmina longirostris	1,464,000	2(+M+F)	June 21
Ceriodaphnia lacustris	60,000	6(-M-F)	Aug. 11
Ceriodaphnia sp.	288,000	8(+M-F)	Aug. 26
Chydorus sphaericus	344,000	2(+M+F)	Aug. 11
Daphnia ambigua	200	7(+M-F)	June 2
Daphnia dubia	2,700	8(+M-F)	June 30
Daphnia galeata mendotae	149,000	8(+M-F)	July 15
Daphnia pulex	37,600	6(-M-F)	June 21
Daphnia retrocurva	9,000	6(-M-F)	Aug. 11
Diaphanosoma brachyurum	230	1(+M+F)	June 2
Eubosmina coregoni	10,300	7(+M-F)	Aug. 26
Eurycercus lamellatus	4,300	6(-M-F)	June 21
Latona setifera	130	7(+M-F)	June 21
Leptodora kindtii	1,250	7(+M-F)	Aug. 26
Polyphemus pediculus	5,300	5(-M-F)	July 29
Scapholeberis kingii	200	8(+M-F)	June 2
Sida crystalina	1,900	1(+M+F)	June 21
Simocephalus serrulatus	800	7(+M-F)	May 17
Diaphanosoma bergei	30,000	6(-M-F)	Aug. 11
Calanoid copepodids	33,800	6(-M-F)	July 29
Diaptomus oregonensis	81,000	6(-M-F)	Aug. 11
Calanoid nauplii	12,600	8(+M-F)	Aug. 11
Cyclopoid copepodids	242,000	1(+M+F)	May 17
Cyclops bicuspidatus thomasii	2,000	1(+M+F)	May 17
Cyclops vernalis	6,100	8(+M-F)	May 17
Eucyclops agilus	4,000	3(-M+F)	Sept. 7
Eucyclops speratus	1,000	2(+M+F)	June 21
Macrocyclops albidus	400	7(+M-F)	June 2
Mesocyclops edax	12,000	2(+M+F)	Aug. 11
Tropocyclops prasinus mexicanus	108,000	2(+M+F)	Aug. 11
Cyclopoid nauplii	136,000	2(+M+F)	Aug. 11

Table 5 Average lengths (mm) of dominant zooplankters in enclosures in the presence and absence of zooplanktivores. Data from the main lake adjacent to the enclosures were included in the "planktivores present" category.

	(mm ± 1 St. Dev.) **Planktivores Present**	**Planktivores Absent**
Daphnia galeata mendotae	1.089 ± 0.115	1.171 ± 0.202
Daphnia pulex	0.932 (1 sample)	1.142 ± 0.242
Daphnia retrocurva	0.781 ± 0.131	0.818 ± 0.127
Cyclops vernalis	0.815 ± 0.064*	0.949 ± 0.134
Mesocyclops edax	0.856 ± 0.079*	1.118 ± 0.221
Tropocyclops prasinus mexicanus	0.468 ± 0.028*	0.507 ± 0.023
Diaptomus oregonensis	1.146 ± 0.09*	1.246 ± 0.085

* significantly different according to Student's t-test ($\alpha = 0.05$)

Table 6 Biomass/biovolume of *Daphnia* spp. and several phytoplankton species in eight enclosures in Rice Lake showing effects of addition and removal of planktivorous yellow perch. Values are averages for the early summer (May-June) and late summer (Aug.-Sept.) periods. Asterisks (*) indicate apparently strong trophic effects (biomass difference $\geq$ 4X).

	May - June Enclosures		Aug - Sept Enclosures	
	1,2,3,4 (fish added)	5,6,7,8 (fish removed)	1,2,3,4 (fish added)	5,6,7,8 (fish removed)
**Daphnia* spp. ($mg \cdot m^{-3}$)	<0.5	115	1	360
*Phytoplankton (total) ($mm^3 \cdot m^{-3}$)	3,280	500	11,890	12,120
*Bacillariophyceae	1,500	270	2,460	1,190
Achnanthes	5	3	40	20
**Asterionella*	330	15	0	0
**Epithemia*	5	0	140	5
Fragilaria	30	10	35	25
Gomphonema	0	3	0	75
**Melosira*	620	190	2,040	910
Rhopalodia	0	0	35	130
**Tabellaria*	20	5	0	0
*Chlorophyceae (excl. filamentous)	250	70	310	150
**Mougeotia* and *Oedogonium*	1,250	20	940	330
Chrysophyceae	140	50	45	30
Cryptophyceae	25	50	100	190
Cyanophyceae	100	40	7,650	9,930
Anabaena	20	30	5,200	9,220
Aphanizomenon	0	1	1,260	350
**Lyngbya*	5	0	160	50
**Microcystis*	2	0	420	80
**Oscillatoria*	65	1	500	170
*Dinophyceae	20	5	370	290

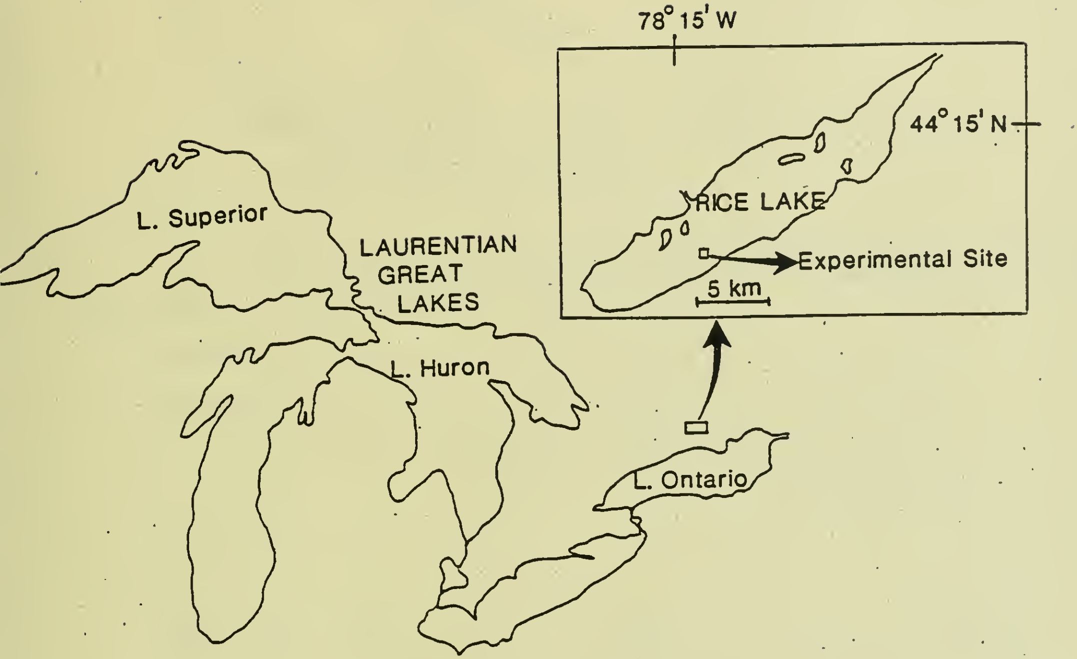

Fig. 1. Map showing the location of the study area in southern Ontario.

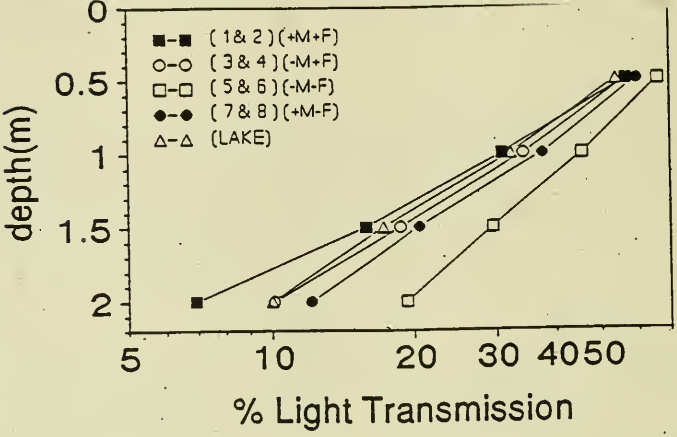

Fig. 2. Percentage light (PAR) transmission at four depths in enclosures 1-8 and at the Rice Lake reference (non-enclosed) cite. Pairs of data from enclosures with like treatments (keyed as in Table 1) have been averaged over the May to September period of the experiment.

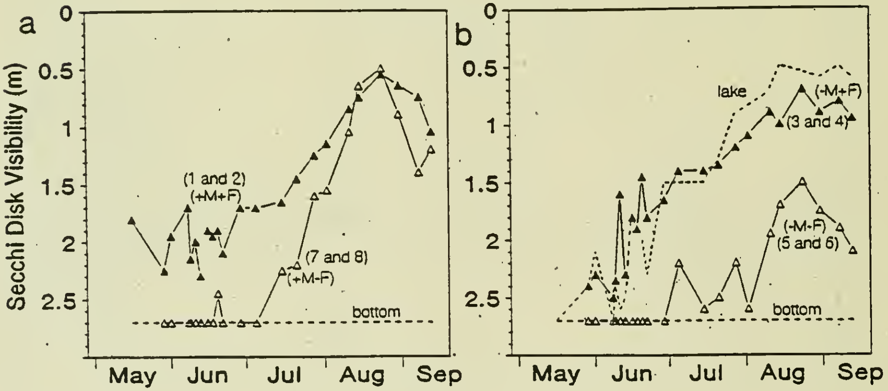

Fig. 3. Secchi disc visibilities in enclosures 1, 2, 7 and 8 (a) and 3-6 (b) and at the unenclosed reference (lake) site (keyed as in Table 1). Pairs of data from enclosures with like treatments have been averaged for each sampling date.

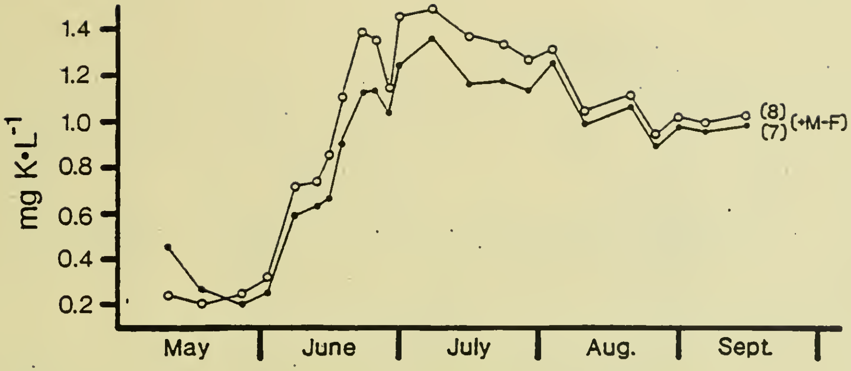

Fig. 4. Changes in potassium concentrations in enclosures 7 and 8, showing agreement between duplicate treatments (macrophytes present, zooplanktivores removed).

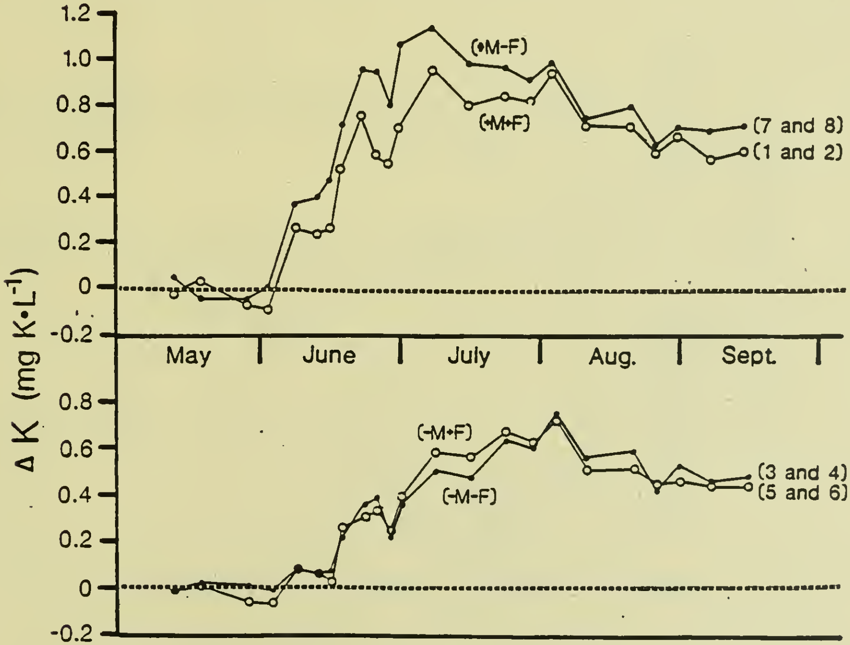

Fig. 5. Changes in potassium concentrations (from initial zero baseline) in enclosures with and without macrophytes and zooplanktivores (keyed as in Table 1). Data plotted for each pair of replicate treatments are the arithmetic means.

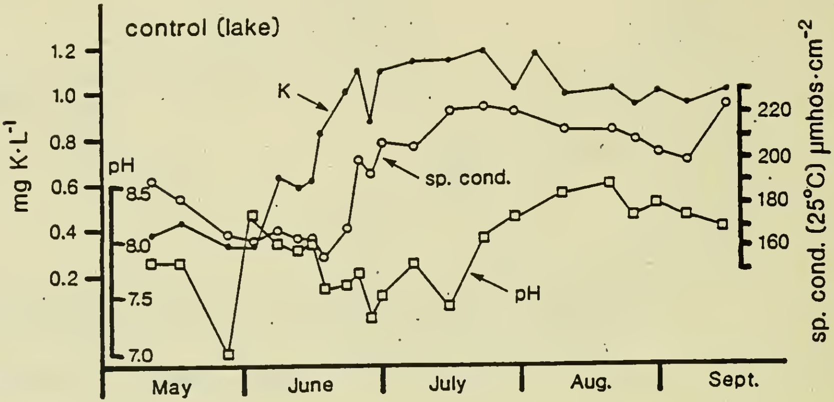

Fig. 6. Specific conductance (25°C), potassium and pH changes at a nearby reference (unenclosed) site in Rice Lake.

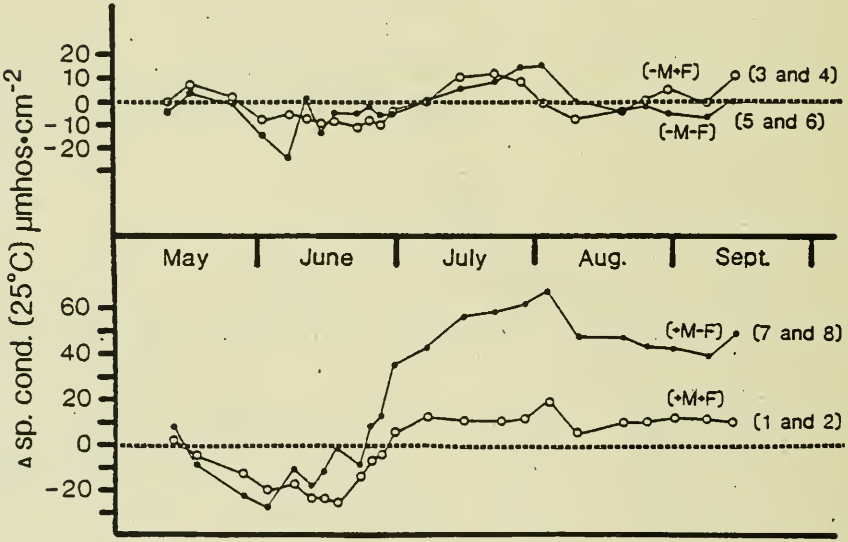

Fig. 7. Changes in specific conductance (from initial zero baseline) in enclosures with and without macrophytes and zooplanktivores (keyed as in Table 1). Data plotted for each pair of replicates are the arithmetic means.

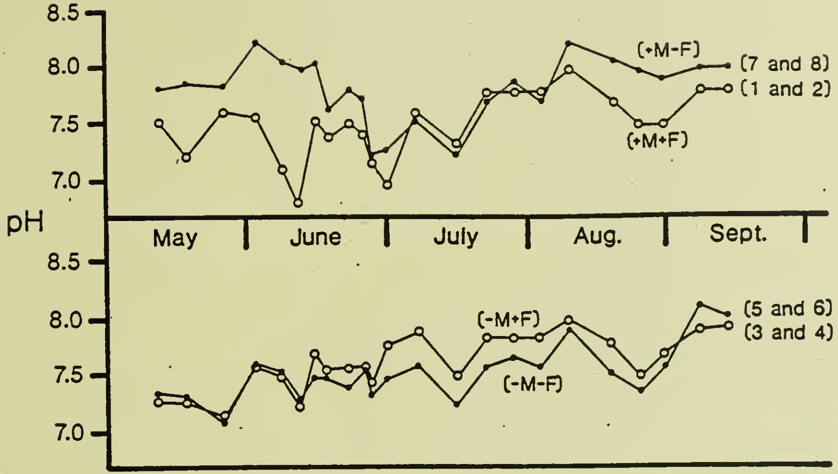

Fig. 8. Changes in pH in enclosures with and without macrophytes and zooplanktivores (keyed as in Table 1).

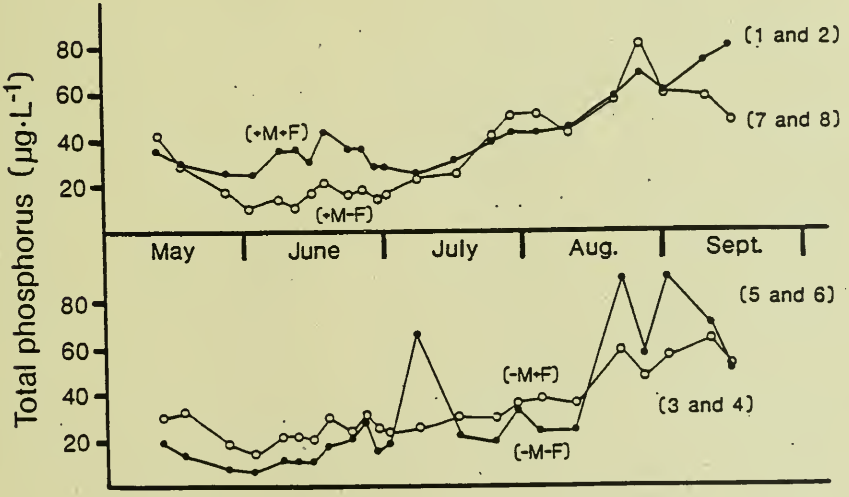

Fig. 9. Changes in total phosphorus in enclosures with and without macrophytes and zooplanktivores (keyed as in Table 1).

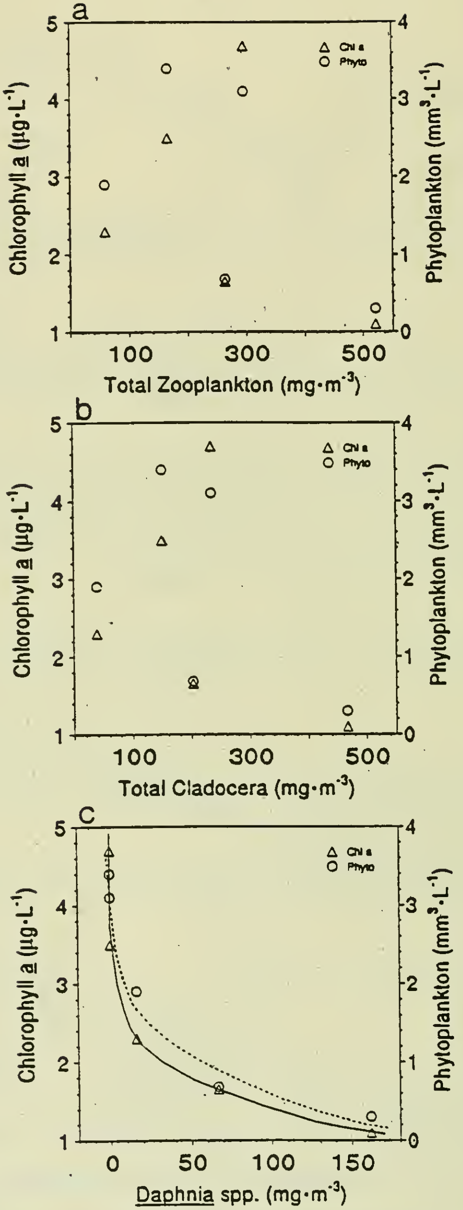

Fig. 10. Total crustacean zooplankton (a), cladoceran (b) and Daphnia (c) biomass (dry mass) relationships with chlorophyll a and phytoplankton biovolume for the four enclosure treatments and the Rice Lake reference site; May-June averaged data.